MIGRATORY CONNECTIVITY AND PHILOPATRY OF COWNOSE RAYS *RHINOPTERA BONASUS* ALONG THE ATLANTIC COAST, USA

Matthew B. Ogburn[1*], Charles W. Bangley[1], Robert Aguilar[1], Robert A. Fisher[2], Mary Carla Curran[3], Sarah Fae Webb[3], Anson H. Hines[1]

[1]Smithsonian Environmental Research Center, 647 Contees Wharf Road, Edgewater, MD 21037

[2]Virginia Institute of Marine Science, College of William and Mary, P.O. Box 1346, Gloucester Point, Virginia 23062

[3]Savannah State University, Box 20467, Savannah, GA 31404

*Corresponding author email: ogburnm@si.edu

Key words: Migration, Connectivity, Behavior, Acoustic Telemetry, Philopatry, Fisheries Management, Conservation, *Rhinoptera bonasus*

ABSTRACT

Migratory species link spatially separated ecosystems, and understanding their migrations is critical for conservation and management. The cownose ray *Rhinoptera bonasus* is a large-bodied batoid ray implicated in shellfish declines along the US Atlantic coast, but its migrations and habitat use remain poorly understood. We used passive acoustic telemetry to track tagged adult female (N = 30) and male (N = 12) rays released during summer and fall 2014-2016 in Maryland, Virginia, and Georgia. Twenty-three tags provided data for more than one year. Individuals from all tagging locations overwintered in the same region offshore of Cape Canaveral, Florida, then returned in summer to the estuaries where tagging took place. Hidden Markov modeling identified three behavioral states (Resident, Ranging, Migratory), with ray movements generally classified as non-migratory (Resident and Ranging behavioral states) in summer and winter, and migratory (Migratory behavioral state) in spring and fall. Linear discriminate analysis suggested strong philopatry to tagging locations. This study provides the first full annual migration tracks for cownose rays along the US Atlantic coast, indicating that they migrate between summer pupping and mating habitats in estuaries south of Long Island, New York and shared overwintering habitats off the east coast of Florida near Cape Canaveral. Our results highlight the value of national-scale networks of acoustic telemetry arrays for identifying migratory patterns of highly mobile marine species.

INTRODUCTION

Many migratory species move between two or more seasonal habitats, often traveling great distances during annual migrations. This connectivity is critical to ecological and evolutionary processes of migratory species and the ecosystems they inhabit (Harden-Jones 1968, Webster et al. 2002, Webster & Marra 2005, Secor 2015). Information on migratory routes, migration timing, habitat use, and behavior are essential elements of conservation and management strategies for these species and their ecosystems (Webster & Marra 2005, Lascelles et al. 2014). Migratory species may encounter a range of threats and may occur in multiple management jurisdictions at different times of year or during different life-history stages (Lascelles et al. 2014, Heupel et al. 2015). In marine systems, elasmobranch fishes provide a model system for understanding the conservation and management of migratory species with strong ecological interactions (Heupel et al. 2014). Many elasmobranchs are long-lived and exhibit philopatry, repeatedly returning to particular locations (Mayr 1963). This raises the possibility that localized fisheries or other human activities could impact regional stocks and that population recovery could be slow (Heuter et al. 2005, Chapman et al. 2015, Flowers et al. 2016). Elasmobranchs also have the potential to structure marine ecosystems through top-down regulatory effects (Frid et al. 2007, Myers et al. 2007, Wirsing & Heithaus 2007, Wirsing et al. 2007, but see Heupel et al. 2015, Grubbs et al. 2016).

The cownose ray *Rhinoptera bonasus* is a large-bodied, batoid ray that occurs in temperate and tropical coastal waters of the Atlantic Ocean and Gulf of Mexico (Schwartz 1990), with the US Atlantic and Gulf coast populations belonging to genetically distinct stocks (McDowell & Fisher 2013, Carney et al. 2017). In Chesapeake Bay, females mature at age 7-8 years and have a maximum observed age of 21 years at a disc width (DW) of 110.5 cm, and males mature at age

6-7 years with a maximum observed age of 18 years at a DW of 98 cm (Fisher et al. 2013). Cownose rays arrive in mixed schools in May (Smith & Merriner 1987), give birth to a single pup (occasionally two pups [Fisher et al. 2014]) in June or early July, and mate within a few weeks of pupping (Fisher 2010, Fisher et al. 2013). After mating, females remain in Chesapeake Bay until September or October, whereas males typically leave the bay in July (Fisher 2010, Omori & Fisher 2017). Rays tagged in Chesapeake Bay were tracked southward during fall to possible overwintering locations off the southeast coast of Florida, with the exception that some males ranged across the continental shelf in late summer north of the Chesapeake Bay before rejoining the females exiting the bay in early fall (late September-early October) for their southern migration (Omori & Fisher 2017). However, prior tagging efforts were limited by short study durations, low spatial accuracy, and small sample sizes (Omori & Fisher 2017), and important aspects of migration and habitat use such as the full annual migration cycle and the degree of philopatry remain unknown.

Understanding movement patterns is important to understanding the spatial and temporal dynamics of interactions between cownose rays and other components of coastal ecosystems. The limited studies conducted to date suggest that cownose ray foraging activity can structure benthic communities including facilitating increased bivalve functional diversity (Glaspie & Seitz 2017), reducing local populations of wild and aquaculture bivalves (Merriner & Smith 1979, Peterson et al. 2001, Myers et al. 2007, Mann et al. 2016), and uprooting seagrass beds (Orth 1975, Townsend & Fonseca 1998). Diet data suggest that foraging efforts primarily target soft and hard-shelled clams in soft sediments (Smith & Merriner 1985, Fisher 2010, Fisher et al. 2011, Bade 2014), along with other epibenthic and infaunal invertebrates (Collins et al. 2007b, Ajemian & Powers 2012).

Management jurisdictions along the US Atlantic coast do not currently have fishery management plans for cownose rays, but expanding recreational fisheries (in which a large proportion of cownose rays are harvested for sport) are driving interest in development of management and conservation initiatives. Sport fisheries have increased in part because cownose rays were implicated in declines in US shellfish populations resulting from trophic release due to overharvesting of large coastal sharks (Myers et al. 2007). However, Grubbs et al. (2016) reviewed this hypothesis and concluded that overharvest followed by disease, rather than cownose ray predation, better explains shellfish declines. Regardless, development of management and conservation plans will require information on migration and habitat use to determine appropriate spatial scales for management. In particular, geographically focused fishing (recreational or commercial) could have a disproportionate effect on segments of the population if cownose rays exhibit strong natal philopatry and catches occur during the reproductive season. Such movement studies can be costly and should be conducted strategically (McGowan & Possingham 2016, McGowan et al. 2017). For cownose rays, acoustic telemetry provides a cost effective method for obtaining critical information on migratory behaviors, understanding the extent of philopatry and other patterns of habitat use, and evaluating the potential costs of not incorporating movement behaviors into management plans (Ogburn et al. 2017). The objectives of the present study were: 1) to document patterns of migratory connectivity and habitat use of adult cownose rays in the western Atlantic, 2) to identify periods of migration and residence, and 3) to evaluate the extent of philopatry during summer and winter. We also address implications for conservation and management of cownose rays along the US Atlantic coast.

MATERIALS AND METHODS

Tagging, tag retention, and survival

Mature cownose rays were tagged at three locations in Chesapeake Bay during May through October 2014, 2015, and 2016 (Fig. 1). Commercial fishers captured rays using haul seines or pound nets, in which they are a common component of the bycatch. The venomous barbs were carefully clipped off upon obtaining rays from fishers to limit potential harm to each other and to researchers following best practices for handling stingrays (Marshall et al. 2017). Rays were then transferred to temporary holding tanks prior to tagging, although holding procedures differed slightly between Virginia and Maryland tagging events.

In Virginia, haul seines were fished from Hampton to Goodwin Neck, including Poquoson River and Back River. Fishers placed captured rays in large insulated holding totes onboard commercial fishing vessels with continuous flow of ambient water until off-loading (1-2 h). Live rays were transferred to large holding totes on a pickup truck and transported to a partial re-circulating holding tank measuring 4.3 m x 6.4 m and a depth of 0.71 m at the Virginia Institute of Marine Science (VIMS) and monitored for 24-72 h.

Prior to tagging, healthy rays were transferred to small (1.5-m diameter) wading pools and anaesthetized using MS222 following Omori & Fisher (2017). Concentrations of 75 mg l^{-1} were used initially, with a shift to 100 mg l^{-1} to reduce the time to anesthesia. Rays reached anesthetic stage III (after Coyle et al. 2004) for surgery after 8.5-15 minutes for MS222 dosage of 75 mg l^{-1} and 5.5-13 minutes for 100-mg l^{-1} dosages (after Coyle et al. 2004). Once anesthetized, rays were positioned ventral side up onto a flat, padded platform with adjustable elastic cord stretched and secured over both pectoral fins to provide support during surgery. The surgery platform was positioned and secured in the water at an angle (~20-25°) in which the ray head, spiral valves, and gill slits were submerged in water containing anesthetic but the incision site was above the water line. The incision site was treated with Betadine and an 18-25 mm incision was made through the abdominal wall with a sterilized surgical knife located approximately 100 mm anterior of the cloacal opening and 50 mm to the anatomical right side of the ventral midline. An incision to the right of midline was favored based on female cownose ray reproductive anatomy, with the right uterus vestigial within their paired oviducts providing more space in the abdominal cavity during late stages of gestation. The incision site in males matched that of females though males have functionality from both paired reproductive organs. A VEMCO 69 kHz V13 or V16 acoustic transmitter coated with antibiotic gel was implanted in the abdominal cavity and the incision was closed with 3-4 simple interrupted sutured using synthetic absorbable suture material (Ethicon Size 0 PDS II suture, with a 36 mm OS-6 reverse cutting needle). Directly after the tagging procedure, we recorded ray disc width (DW) and sex, and inserted a uniquely numbered external dart tag into the dorsal surface of the right pectoral fin. We also recorded time for each ray to reach anesthetic stage III (anesthesia time) and the duration of each surgical procedure (surgery time). All tags and surgical equipment were sterilized with Betadine prior to surgery.

After surgery, tagged rays were transferred back into a sectioned off, aerated recovery area within the large holding tank containing ambient water, positioned right-side up, and monitored. We recorded the time between placement in holding tank and return to normal swimming behavior for each ray (recovery time). Recovery time ranged from 4.5-12 minutes for MS222 dosage of 75 mg l^{-1} and 11.5-19 minutes for 100 mg l^{-1} dosages. After initial recovery, rays were held for an additional 24-72 h (except on one occasion when three rays were released 5 h postsurgery due to existing extreme environmental conditions). Full recovery from the tagging procedure (e.g., incision healing, swimming ability, overall behavior, etc.), tag loss, and mortality were recorded during the holding period. Rays held for 24-72 h after tagging (N = 37) retained 100% of both internal and external tags. Survival during the post-tagging holding period was 91.2%. The three mortalities were rays that exhibited moderate stress and lethargy after transfer from commercial fishing vessels and which were subsequently deemed suitable for tagging after 24 h in holding tanks. Only rays that appeared healthy and exhibited normal behaviors during the holding period were released in the wild directly adjacent to the holding facility.

In Maryland, fishers captured rays from commercial pound nets located near the mouths of the Choptank and Rhode rivers. Captured rays were transferred to aerated bins and transported to nearby docks (3-5 km) for surgical procedures. A large portable baby pool (2.4-m diameter) was used to hold rays before and after surgeries and a separate 1.3-m diameter tank was used for anesthesia. Surgical, tagging, and data recording procedures were identical to those for Virginia, with the exceptions that surgical tools were sterilized by autoclave and a 100 mg l^{-1} dosage of MS222 was used for all rays. Recovery time was 6.5-19.8 minutes, similar to the recovery time for Virginia rays at the same dosage. Upon recovery to normal swimming behavior, rays were released immediately at the tagging location. Immediate release was used to alleviate stress from additional transport, handling, and holding in tanks.

Two adult male cownose rays were tagged in the Herb River near Savannah, Georgia in 2014. These rays were collected via longline using 2.54-cm circle hooks baited with squid. Each line soaked for approximately 30 minutes before retrieval by kayak. After dehooking, rays were transported to the nearest dock for surgical implantation of a VEMCO V16 acoustic tag. All surgical equipment was rinsed with a 70% ethanol solution and the surgery site on the ray was cleaned with an iodine swab. Rays remained in shallow ambient water during surgery so that water could pass over the gills. A small incision was made on the left ventral side of the abdomen where the tag was inserted and the incision was closed with monofilament dissolvable sutures in two simple interrupted sutures. We recorded disc width, total length, weight, sex, and location of capture if possible, and released rays immediately within 100 m of capture location.

All tagged cownose rays were assigned to tagging regions based on the location where they were tagged and released. Rays tagged within the Chesapeake Bay north of the Maryland state line were grouped in the “MD Chesapeake” tagging region, while those tagged south of the state line were assigned to the “VA Chesapeake” region. Both rays tagged in the Herb River were grouped in the “Savannah” tagging region.

Telemetry and environmental data

Acoustic tag detection data were obtained from multiple acoustic telemetry receiver arrays. At the time of release, rays were initially detected immediately after release using a VEMCO VR2W hydrophone deployed at the VIMS pier or at Maryland sites using a VEMCO VR100 hydrophone. Rays were also detected using SERC-owned VR2W arrays in the Rhode and Patuxent rivers in Maryland and NOAA’s Chesapeake Bay Office Chesapeake Bay Interpretive Buoy System (of which SERC has contributed four VEMCO receivers). Two arrays were monitored in Georgia waters. One array was comprised of 10 VEMCO VR2W passive receivers within the Herb River behind Savannah State University in Savannah as well as an additional 14 receivers within Romerly Marsh Creek near Skidaway Island. All other data were contributed by researchers participating in the Atlantic Cooperative Telemetry (ACT) and Florida Atlantic Coast Telemetry (FACT) networks.

Analysis of telemetry data

Because we wanted to model coastal-scale movement patterns, rays detected over a period of less than 90 days were excluded from subsequent analyses. For each ray, consecutive daily averaged positions were calculated by arithmetically determining the mean latitude and longitude across all receivers detecting that ray each day it was detected. The release date and location were included when calculating daily averaged positions. Distance (km) between consecutive positions was calculated using the spherical law of cosines and travel velocity (km d^{-1}) was calculated by dividing the distance by the number of elapsed days between positions. Distance, velocity, and elapsed days were used as covariates to model the movement behavior of the tagged rays.

Hidden Markov modeling (HMM) was used to classify cownose ray behavioral states. This type of modeling works by identifying hidden underlying states, which can be interpreted as behavioral states for animals, using observable data series such as telemetry detections (Langrock et al. 2012). All HMM procedures were conducted using the package *moveHMM* in R (Michelot et al. 2016, R Core Team), which applies HMM analysis to each tagged animal individually. The package script automatically calculates the turning angle (rad) of the vector between consecutive positions, which was included as a covariate in some of the models. We ran two- and three-state HMMs incorporating all or a subset of covariates, and the combination of covariates providing the greatest log-likelihood values was chosen as the optimal model. Starting parameters were identified by plotting histograms of distance and turning angle for each ray and were modified to match the mean values generated by HMM runs until consecutive runs produced similar means. Normality of HMM distance and turning angle parameters was assessed using pseudo-residual plots.

Behavioral state was assigned using the Viterbi algorithm, which decodes the state based on the most likely state sequence in the HMM (Zucchini et al. 2016). The mean (± standard deviation [SD]) distance, velocity, and elapsed days were calculated in each behavioral state and one-way analysis of variance (ANOVA) and Tukey's Honestly Significant Difference (HSD) procedures were used to determine whether these covariates differed significantly between each state.

To define time periods associated with particular movement behaviors, the robability of each behavioral state, or the differing state if only one showed significant differences from the others, was plotted against the numerical day of year. Time periods were classified as periods of little change in behavioral state, which we defined as periods during which the same behavior state was classified for 50% or more of the individual rays during at least three of a given set of four consecutive daily positions. This was conducted independently for each tagging region to account for geographical differences in migration timing. Periods encompassing days of the year occurring within June-August were considered to represent summer behavior, while those encompassing December-February were considered to represent winter behavior. Once time periods associated with movement behaviors were defined, one-way ANOVA and Tukey's HSD procedures were used to assess differences in latitude and longitude between rays by tagging region during each period.

After periods of summer behavior were defined using HMM, we evaluated whether the location of summer behavior matched the region where each ray was tagged. This was necessary to identify the most likely location of summer habitat use because many tags were deployed in late August-October when rays may have been exhibiting migratory behavior. Mean daily positions were used to classify individual tagged rays to regions based on mean latitude and longitude during the period of summer when movement was at a minimum (May-July). Linear discriminant analysis (LDA) was then used to predict tagging region for each individual daily position during May-July by mean latitude and longitude. LDA was conducted using the "lda" function in the *MASS* package in R. Rays were classified to a particular region if at least 50% of daily positions were classified to that region, and the percentage of daily positions classified to the original assigned tagging region was calculated.

Philopatry was assessed for individual tagged cownose rays that were detected in May through July in multiple years (5 individuals). We compared mean daily positions among years during the months of May through July because it is likely the time of parturition and mating for cownose rays in the Chesapeake Bay (Fisher 2010). These behaviors are associated with natal philopatry in elasmobranch species (Chapman et al. 2015, Flowers et al. 2016). Mean daily position was compared using one-way ANOVA to determine whether differences in mean latitude and longitude during May-July were statistically significant between years.

RESULTS

Tagging and tag detections

A total of 36 mature cownose rays tagged and released from 2014-2016 were detected during more than one day between May 31, 2014 and December 15, 2016 (Table 1). Five individuals were tagged in Maryland Chesapeake waters, two in the Herb River near Savannah, Georgia, and 29 in Virginia Chesapeake Bay waters. Of these, 27 were female and nine were male. Both sexes were represented among MD Chesapeake and VA Chesapeake rays, but both Savannah rays were males. The majority of the rays (24 individuals) were tagged in the summer and early fall of 2014, while 10 were tagged in 2015 and two were tagged during the summer of 2016 (Table 1).

The fate of tagged rays cannot be known for certain, but survival can be inferred from tag detection data and the expected battery life of each tag. Of the 36 cownose rays detected more than one day, 13 (36.1% of the tagged rays) were only detected during the first year of tracking. The remainder were detected over multiple years, with 12 (33.3%) detected over two years and 11 (30.6%) detected over all three years. Seven of the 24 rays tagged in 2014 (29.2%) and three of the 13 rays tagged in 2015 (23.1%) were not detected after the first year of tag deployment. The five Maryland rays were each detected in multiple years. Seven of 19 Virginia rays tagged in 2014 (36.8%) and three of 10 rays tagged in 2015 (30.0%) were not detected in the year following tagging. For eight rays tagged in 2015 and the two rays tagged in 2016, tags remain active and additional detections are expected.

Analysis of telemetry data

Cownose ray tag detections ranged along the U.S. Atlantic coast from Long Island, New York to Port St. Lucie, Florida (Figure 1). Of the 36 tagged rays, 28 were detected over a sufficient time period to be included in HMM analysis. This included five rays from the MD Chesapeake region, 21 from the VA Chesapeake region, and both rays from the Savannah region (Figure 2). Plotting latitude of detection by date showed evidence of an annual migration pattern, with all rays occurring at approximately the latitude of tagging during summer, rapid changes in latitude during the spring and fall, and occurrence within the same narrow latitudinal range of rays from all tag regions during the winter (Figure 3).

The three-state model excluding turning angle but including velocity and elapsed days showed the greatest log-likelihood (Table 2) of the HMM variations attempted. State 1 was defined by short distances (<0.7 km), low velocity, and few elapsed days between detections. State 2 showed moderate mean distance and velocity and elapsed days were similar to State 1. Means of all variables were an order of magnitude higher in State 3 than either of the other behavioral states. Mean distance, velocity, and elapsed days showed that all three movement behavior states were significantly different based on velocity, but differences in distance and elapsed days between States 1 and 2 were not statistically significant (Table 3). Based on these measurements, State 1 was defined as Resident behavior, State 2 as Ranging behavior, and State 3 as Migratory movement. Positions showing Resident and Ranging behavioral states tended to be distributed at the northern and southern extents of individual ray migrations while most positions between these areas were classified as the Migratory behavior state (Figure 4a). Resident and Ranging behavioral states overlapped in latitude, longitude, and time of year as the dominant behavior states during the summer and winter, while the majority of positions during the fall and spring were classified within the Migratory behavioral state (Figure 4b). Because of this and because the Migratory behavioral state was distinct from both Resident and Ranging states, the probability of a given ray exhibiting Migratory behavior was used to delineate migratory or non-migratory time periods.

The periods between days 100 and 250 and days 300 and 350 showed <50% probability of Migratory behavior overall, but timing of the behavioral state switching varied by tagging region (Figure 5). MD Chesapeake rays switched to generally consistent (>50% probability) Migratory behavior between days 5 and 156 and 237 and 341, while VA rays were generally consistently Migratory from the beginning of the year to day 135 and between days 236 and 324. Rays tagged in the Savannah region showed shorter spring (days 5-64) and fall (days 288-333) periods of Migratory behavior than rays from either Chesapeake Bay tagging region. For each tagging region, days with >50% probability of Migratory behaviors were classified as the migratory periods, while dates in which Migratory behavior probability was <50% occurring between days 60 and 290 were classified as summer non-migratory period (hereafter summer) and those between day 300 and day 5 the following year were classified as winter non-migratory period (hereafter winter). Resident behavior was treated as a special subset of non-migratory behavior characterized by minimal movement and occurring in summer or winter.

All cownose rays appeared to occupy the general area offshore of Cape Canaveral, Florida during winter, when mean daily latitude and longitude did not differ significantly between any tagging regions (Table 4, Figure S1). Latitude differed significantly between all tagging regions during summer, but longitude did not differ between the two Chesapeake Bay tagging regions during any season. Daily mean latitude and longitude differed significantly between cownose rays tagged in Savannah and both Chesapeake Bay tagging regions during all seasons except winter (Table 4, Figure S1).

Of the 24 rays with more than one daily position during the May-July period, 18 were classified to their original assigned tagging region based on LDA results. All daily positions of Savannah rays were classified to the Savannah region, but cross-classification occurred between MD

Chesapeake and VA Chesapeake rays (Figure S2). Two rays originally tagged in Maryland waters were classified as VA Chesapeake rays and three rays assigned to the VA Chesapeake region were classified as MD Chesapeake rays (Table 6). Of the rays that were classified to a region different than their original tagging region, two were tagged in August 2014 and three were tagged in October 2015 (Table 5).

Philopatry was evaluated for the five tagged cownose rays that were detected in both 2015 and 2016 during the May-July pupping and mating season (Table 6). Four of these rays were tagged in Virginia Chesapeake Bay waters and one was from the Savannah tagging region (Table 1). Mean latitude and longitude did not differ significantly between years for three of the VA Chesapeake rays, but significant differences were found for the remaining VA Chesapeake ray and the Savannah ray (Table 6). The VA Chesapeake ray inhabited Virginia waters during 2015 and Maryland waters in 2016. In contrast, the mean latitude and longitude for the Savannah ray during both years fell within the same acoustic array, which was spatially limited to the Herb River in Georgia.

DISCUSSION

Location data for individual cownose rays *Rhinoptera bonasus* obtained using acoustic telemetry provided the first full annual migration tracks for the species along the US Atlantic coast, revealing that rays repeatedly migrate between the same overwintering and summer pupping and mating habitats each year. Rays tagged in Maryland, Virginia, and Georgia all overwintered in coastal areas of Florida between Cape Canaveral and St. Lucie Inlet, then dispersed to summer habitats near the tagging locations in each of two annual migrations that occurred during the study period. The general route and timing of migration were consistent with the small number of rays tracked during the fall migration period using PSATs (Grusha 2005, Omori & Fisher 2017). Results of HMM indicated that migrations were punctuated by both winter and summer non-migratory periods, with differences in latitude among rays from different tagging locations only detected during summer. A lack of detections farther south in Florida (Joy Young, personal communication; Fig. 1) is consistent with genetic data indicating separate stocks on the US Atlantic and Gulf coasts (McDowell & Fisher 2013, Carney et al. 2017). This finding also contrasts with a lack of seasonal migration by cownose rays in estuaries of the southwest coast of Florida (Collins et al. 2007a). Telemetry data (Omori & Fisher 2017 and the present study) suggest that the Atlantic coast population of cownose rays may separate into different estuaries in summer and mix during spring and fall migrations and in overwintering habitat along the Atlantic coast of Florida.

The seasonal migrations of individual tagged rays connected estuarine and coastal habitats along >1,500 km of the US Atlantic coast, indicating that ecological interactions (e.g. trophic dynamics, disturbance of seagrass beds, bioturbation), fishing mortality, and interactions with shellfisheries should be evaluated at similar spatiotemporal scales. In summer, latitude was significantly different among rays from different tagging locations, suggesting strong philopatry at scales of <200 km (the distance from Maryland to Virginia tagging locations). This was supported by LDA results, suggesting that 75% of individual rays could be reassigned to their tagging location. A few rays tagged in Virginia showed habitat use more characteristic of Maryland, or vice versa, but these rays were tagged after the mating season and may have been tagged after leaving their primary area of summer residency. In addition, some tagged rays returned to estuarine portions of the same rivers in consecutive summers, often detected on the same acoustic receivers, suggesting the potential for philopatry and fine-scale stock structure. However, the small sample size of rays detected during the period of summer Resident behavior (May-July) in consecutive years (5 individuals) and was too small to draw strong conclusions about philopatry and additional telemetry and population genetic data are needed to evaluate stock structure. Similar patterns of high site fidelity to summer habitats have been observed in other estuarine elasmobranchs including the Atlantic Stingray *Dasyatis sabina* (Ramsden et al. 2017).

With the growing interest in managing cownose ray populations along the US Atlantic coast whether to conserve ray populations or reduce negative interactions with shellfisheries, there is an urgent need for detailed information on habitat use, habitat connectivity, and population structure. Targeted fisheries and bycatch during summer, especially in early summer during pupping and mating, have the potential to cause local extirpation and reduce genetic diversity depending on the scale of philopatry. In contrast, genetic data from three adjacent Chesapeake Bay tributaries during summer failed to detect fine-scale stock structure (Carney et al. 2017). Nevertheless, adult male and female rays tagged in three coastal states returned to areas near the tagging locations in each of two full annual migration cycles, indicating that philopatry and stock structure likely exist at spatial scales at least as small as state management jurisdictions. A coastwide assessment of stock structure during the pupping and mating season should be a high priority to determine the appropriate spatial scale of management and conservation during summer.

During winter, tagged rays from all locations occurred along the Florida east coast from Cape Canaveral to St. Lucie Inlet, an area that probably represents essential habitat for the population. The northern extent of the winter habitat is likely determined by water temperature, whereas the eastern and southern extents could be defined by the shelf break, prey availability, or some unknown factor. Although cownose rays do inhabit the Indian River Lagoon (Snelson 1981, 1983, Schmid et al. 1988), none of our tagged rays was detected within the extensive acoustic receiver array there (Joy Young, personal communication). Female and male rays tend to occur at deeper water depths (10-20 m) in winter than in summer (typically 0-10 m) (Omori & Fisher 2017), but little is known about their ecology during winter. The Atlantic coast of Florida is also used as overwintering habitat by other coastal migratory elasmobranchs, including juvenile sand tigers *Carcharias taurus* (Kneebone et al. 2014), blacktip shark *Carcharinus limbatus* (Castro 1996), and juvenile lemon shark *Negaprion brevirostris* (Reyier et al. 2014). Improving our understanding of the distribution and ecology of cownose rays in Florida coastal ecosystems in winter will be valuable to understanding the ecology of and management options for the Atlantic coast population.

Spring and fall migrations concentrate ecological and fishery interactions in coastal and nearshore areas. Cownose rays are perhaps most widely known as predators on shellfish in coastal bays and lagoons like those in North Carolina (Peterson et al. 2001, Myers et al. 2007), although they were not the primary cause of declining shellfisheries (Grubbs et al. 2016). Regardless, large migrating schools of cownose rays are likely to have strong ecological interactions as they move through habitats along the coast (Orth et al. 1975, Peterson et al. 2001). Some rays tagged in Maryland and Virginia did pass through North Carolina lagoons on both the northward and southward migrations, confirming that migrating individuals from northern locations do move through areas where rays have been observed feeding on scallops in spring and fall. Management of fisheries targeting cownose rays or efforts to mitigate interactions with shellfisheries by population control during the migratory seasons are complicated by the difficulty of distinguishing which segment of the population is present at a given time and location. Because of this problem, mitigation measures to protect shellfish from ray foraging are more promising than population control for minimizing the impact of migrating rays on shellfisheries.

State-space modeling improves upon previous mechanistic modeling approaches to animal movement behavior by allowing for the incorporation of other environmental or behavioral factors (Patterson et al. 2008). In an animal movement context, hidden Markov modeling uses variables from telemetry data such as location, distance between detections, and turning angle over a time series to determine the most likely behavioral state based on the relationships between these variables (Zucchini et al. 2016). Other non-telemetry data such as environmental conditions or known aspects of the animal's behavior can also be incorporated into the HMM process (Jonsen et al. 2013). In our approach, it was informative to include calculated travel velocities and time between tag detections, which added behavioral dimensions to the standard telemetry metrics. The significant difference in velocity between Resident and Ranging behavioral states suggests localized complexity in movement behavior during non-migratory periods that is worthy of further attention. However, the low frequency, relatively low precision data provided by acoustic telemetry relative to satellite telemetry likely limited our ability to detect fine-scale movement behaviors. For example, turning angle was likely not included in our best-performing models because the coastwide spatial scale of our analysis, daily averaging of positions, and limited spatial coverage of acoustic receivers (Figure S3) prevented us from detecting increased tortuosity of movement that could be indicative of fine scale behaviors like foraging (Benhamou & Bovet 1989). Despite the drawbacks of acoustic telemetry data for state-space modeling, the HMM process did appear to be effective at differentiating coarse-scale movement patterns related to migratory vs. non-migratory behaviors for a species that undergoes long-distance annual migrations.

This study provides the first data for full annual migration cycles of cownose rays along the US Atlantic coast, indicating that they undergo migrations between summer habitats in estuaries south of Long Island and winter habitats along the coast of Florida near Cape Canaveral. Our tagged rays from Chesapeake Bay and Georgia overwintered in the same area and separated during the early summer pupping and mating season into the estuaries where they were tagged, which is suggestive of population structure that warrants additional attention for its potential importance in the design of management strategies. Rays detected in consecutive summers exhibited strong philopatry to the estuary where they were tagged. Until the stock structure is better understood, management should focus on minimizing fishery removals during summer resident period, especially during pupping and mating (May-July), to protect phenotypic and genetic diversity. Managers should also recognize that stocks are mixed in other seasons such that fishery removals during fall, spring, and especially winter could impact much or all of the population. Finally, our results highlight the value of large-scale networks of acoustic telemetry arrays for tracking migrations of highly mobile marine species.

ACKNOWLEDGEMENTS

We thank C. Brinton, C. Corrick, N. Fisher, M. Goodison, K. Heggie, J. Kirkham, M. Kramer, K. Parsons, C. Peterson, S. Ramsden, K. Richie, R. Semmler, M. Sherman, C.J. Sweetman, and several commercial watermen for technical assistance capturing and tagging rays. We also thank the coordinators of the ACT (L. Brown) and FACT (J. Young) networks and many researchers for sending tag detection data, especially E. Reyier (Kennedy Space Center Ecological Program), I. Park (DE Department of Natural Resources), D. Fox (Delaware State University), R. Rulifson (East Carolina University), M. Ajemian (Florida Atlantic University Harbor Branch Oceanographic Institute), C. Kalinowsky (GA Department of Natural Resources), J. Krause (North Carolina State University Center for Marine Science and Technology), K. Schabow (NOAA Chesapeake Bay Office), D. Zapf (NC Division of Marine Fisheries), M. Arendt, B. Frazier, and M. Hart (SC Department of Natural Resources), K. Dunton (Stony Brook University), M. Benevides (University of North Carolina Institute for Marine Science), D. Secor and M. O'Brien (University of Maryland Chesapeake Biological Laboratory), C. Watterson (US Navy), and M. Fisher (Virginia Institute of Marine Science). We offer special thanks to A.-L. Harrison for providing assistance with analysis of detection data. Two anonymous reviewers provided comments that substantially improved the manuscript. In Chesapeake Bay, funding was provided by the Smithsonian Institution Office of the Undersecretary for Science. C. Bangley was supported on a Smithsonian Movement of Life Initiative postdoctoral fellowship funded by Aramco Services Company. In Georgia, funding was provided by the National Science Foundation GK-12 award (#DGE-0841372) and the Department of Education Title VII (#P382G090003), and some receivers were provided by The Nature Conservancy.

LITERATURE CITED

Ajemian MJ, Powers SP (2012) Habitat-specific feeding by cownose rays (*Rhinoptera bonasus*) of the northern Gulf of Mexico. Environ Biol Fishes 95:79–97

Bade LB, Balakrishnan CN, Pilgrim EM, McRae SB, Luczkovich JJ (2014) A genetic technique to identify the diet of cownose rays, *Rhinoptera bonasus*: analysis of shellfish prey items from North Carolina and Virginia. Env Biol Fish 97:999-1012

Benhamou S, Bovet P (1989) How animals use their environment: a new look at kinesis. Anim Behav 38:357–383

Carney SL, McVeigh DM, Moss JB, Ferrier MD, Morrissey JF (2017) Insights on mitochondrial genetic variation in Chesapeake Bay summer-resident Cownose Rays. Trans Am Fish Soc 146:478–484

Castro JI (1996) Biology of the blacktip shark, *Carcharinus limbatus*, off the Southeastern United States. Bull Mar Sci 59:508–522

Chapman D, Feldheim KA, Papastamatiou YP, Hueter RE (2015) There and back again: A review of residency and return migrations in sharks, with implications for population structure and management. Annu Rev Mar Sci 7:547–570

Collins AB, Heupel MR, Motta PJ (2007a) Residence and movement patterns of cownose rays *Rhinoptera bonasus* within a south-west Florida estuary. J Fish Biol 71:1159–1178

Collins AB, Heupel MR, Hueter RE, Motta PJ (2007b) Hard prey specialists or opportunistic generalists? An examination of the diet of the Cownose Ray, *Rhinoptera bonasus*. Mar Freshw Res 58:135–144

Coyle SD, Durborow RM, Tidwell JH (2004) Anesthetics in aquaculture. Southern Regional Aquaculture Center, Publication No.3900, Stoneville

Fisher RA (2010) Life history, trophic ecology, and prey handling by Cownose Ray, *Rhinoptera bonasus*, from Chesapeake Bay. Virginia Institute of Marine Science, Virginia Sea Grant, Report 2010-20, VSG-10-25, Gloucester Point

Fisher RA, Call GR, Grubbs D (2011) Cownose Ray (*Rhinoptera bonasus*) predation relative to bivalve ontogeny. J Shellfish Res 30:187–196

Fisher RA, Call GC, Grubbs RD (2013) Age, growth, and reproductive biology of Cownose Rays in Chesapeake Bay. Mar Coast Fish 5:224–235

Fisher RA, Call GC, McDowell JR (2014) Reproductive variations in cownose rays (*Rhinoptera bonasus*) from Chesapeake Bay. Environ Biol Fishes 97:1031–1038

Flowers KI, Ajemian MJ, Bassos-Hull K, Feldheim KA, Hueter RE, Papastamatiou YP, Chapman DD (2016) A review of batoid philopatry, with implications for future research and population management. Mar Ecol Prog Ser 562:251–261

Frid AL, Dill M, Thorne RE, Blundell GM (2007). Inferring prey perception of relative danger in large-scale marine systems. Evol Ecol Res 9:635–649

Glaspie CN, Seitz RD (2017) Role of habitat and predators in maintaining functional diversity of estuarine bivalves. Mar Ecol Prog Ser 570:113–125

Grubbs RD, Carlson JK, Romine JG, Curtis TH, McElroy WD, McCandless CT, Cotton CF, Musick JA (2016) Critical assessment and ramifications of a purported marine trophic cascade. Sci Rep 6:20970

Grusha DS (2005) Investigation into the life history of the cownose ray, *Rhinoptera bonasus* (Mitchill 1815). M. S. Thesis, Virginia Institute of Marine Science, College of William and Mary, Williamsburg

Harden-Jones FR (1968) Fish migration. Edward Arnold, London

Heupel MR, Knip DM, Simpfendorfer CA, Dulvy NK (2014) Sizing up the ecological role of sharks as predators. Mar Ecol Prog Ser 495:291–298

Heupel MR, Simpfendorfer CA, Espinoza M, Smoothey AF, Tobin A, Peddemors (2015) Conservation challenges of sharks with continental scale migrations. Front Mar Sci 2:12.

Hueter RE, Heupel MR, Heist EJ, Keeney DB (2005) Evidence of philopatry in sharks and implications for the management of shark fisheries. J Northwest Atl Fish Sci 35:239–247.

Jonsen ID, Basson M, Bestley S, Bravington MV, Patterson TA, Pederson MW, Thomson R, Thygesen UH, Wotherspoon SJ (2013) State-space models for bio-loggers: A methodological road map. Deep Sea Res II 88–89:34–46

Kneebone J, Chisholm J, Skomal G (2014) Movement patterns of juvenile sand tigers (*Carcharias taurus*) along the east coast of the USA. Mar Biol 161:1149–1163

Langrock R, King R, Matthiopaulous J, Thomas L, Fortin D, Morales JM (2012) Flexible and practical modeling of animal telemetry data: hidden Markov models and extensions. Ecol 93:2336-2342.

Lascelles B, Di Sciara GN, Agardy T, Cuttelod A, Eckert S, Glowka L, Hoyt E, Llewellyn F, Louzao M, Ridoux V, Tetley MJ (2014) Migratory marine species: Their status, threats and conservation management needs. Aquat Conserv 24:111–127

Mann R, Southworth M, Fisher RA, Wesson JA, Erskine AJ, Leggett T (2016) Oyster planting protocols to deter losses to cownose ray predation. J Shellfish Res 35:127–136

Marshall A, Marshall B, Smith M (2017) Diving with and handling elasmobranchs. In: Smith M, Warmolts D, Thoney D, Hueter R, Murray M, Ezcurra J (eds) Elasmobranch husbandry manual II: recent advances in the care of sharks, rays and their relatives. Ohio Biological Survey, Inc., Columbus, pp 197–207

Mayr E (1963) Animal Species and Evolution. Belknap Press of Harvard University Press, Cambridge

McDowell JR, Fisher RA (2013) Discrimination of Cownose Ray, *Rhinoptera bonasus*, stocks based on microsatellite DNA markers. NOAA Final Report (NA11NMF4570215) and Virginia Institute of Marine Science, College of William and Mary, Marine Resource Report 2013-8, Gloucester Point

McGowan J, Possingham HP (2016) Commentary: Linking movement ecology with wildlife management and conservation. Front Ecol Evol 4:30.

McGowan J, Beger M, Lewison RL, Harcourt R, Campbell H, Priest M, Dwyer RG, Lin H-Y, Lentini P, Dudgeon C, McMahon C, Watts M, Possingham HP (2017) Integrating research using animal-borne telemetry with the needs of conservation management. J Appl Ecol 54:423–429

Merriner JV, Smith JW (1979) A report to the oyster industry on the biology and management of the cownose ray (*Rhinoptera bonasus*, Mitchill) in lower Chesapeake Bay. Special Report in Applied Marine Science and Ocean Engineering 216. Virginia Institute of Marine Science, Gloucester Point

Michelot T, Langrock R, Patterson TA (2016) moveHMM: An R package for the statistical modelling of animal movement data using hidden Markov models. Meth Ecol Evol 7:1308–1315

Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH (2007) Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science 315:1846–1850

Ogburn MB, Harrison A-L, Whoriskey FG, Cooke SJ, Mills Flemming JE, Torres LG (2017) Addressing challenges in the application of animal movement ecology to aquatic conservation and management. Front Mar Sci 4:70

Omori KL, Fisher RA (2017) Summer and fall movement of cownose ray, *Rhinoptera bonasus*, along the east coast of United States observed with pop-up satellite tags. Environ Biol Fishes 100:1435–1449

Orth RJ (1975) Destruction of eelgrass *Zostera marina* by the cownose ray *Rhinoptera bonasus* in the Chesapeake Bay. Chesap Sci 16:205–208

Patterson TA, Thomas L, Wilcox C, Ovaskainen O, Matthiopolous J (2008) State-space models of individual animal movements. Trends Ecol Evol 23:87–94

Peterson CH, Fodrie JF, Summerson HC, Powers SP (2001) Site-specific and density-dependent extinction of prey by schooling rays: generation of a population sink in top-quality habitat for bay scallops. Oecologia, 129:349–356

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available: https://www.R-project.org

Ramsden S, Cotton CF, Curran MC (2017) Using acoustic telemetry to assess patterns in the seasonal residency of the Atlantic stingray *Dasyatis sabina*. Environ Biol Fishes 100:89–98

Reyier EA, Franks BR, Chapman DD, Scheidt DM, Stolen ED, Gruber SH (2014) Regional-scale migrations and habitat use of juvenile lemon sharks (*Negaprion brevirostris*) in the US South Atlantic. PLOS ONE 9:e88470.

Schwartz FJ (1990) Mass migratory congregations and movements of several species of cownose rays, genus *Rhinoptera*: A world-wide view. J Elisha Mitchell Sci Soc 106:10–13

Secor DH (2015) Migration ecology of marine fishes. Johns Hopkins University Press, Baltimore

Smith JW, Merriner JV (1985) Food habits and feeding behavior of the cownose ray, *Rhinoptera bonasus*, in lower Chesapeake Bay. Estuar Coast 8:305–310

Smith JW, Merriner JV (1987) Age and growth, movements and distribution of the cownose ray, *Rhinoptera bonasus*, in Chesapeake Bay. Estuaries 10:153–164

Townsend EC, Fonseca MS (1998) Bioturbation as a potential mechanism influencing spatial heterogeneity of North Carolina seagrass beds. Mar Ecol Prog Ser 169:123–132

Webster MS, Marra PP (2005) The importance of understanding migratory connectivity and seasonal interactions. In: Greenberg R and Marra PP (eds) Birds of two worlds: the ecology and evolution of migration*.* Johns Hopkins University Press, Baltimore, p 199–209

Webster MS, Marra PP, Haig SM, Bensch S, Holmes RT (2002) Links between worlds: unraveling migratory connectivity. Trends Ecol Evol 17:76–83

Wirsing AJ, Heithaus MR (2007) Living on the edge: dugongs prefer to forage in microhabitats allowing for escape from rather than avoidance of predators. Anim Behav 74:93–101

Wirsing AJ, Heithaus MR, Dill LM (2007) Fear factor: do dugongs (*Dugong dugon*) trade food for safety from tiger sharks (*Galeocerdo cuvier*)? Oecologia 153:1031–1040

Zucchini W, MacDonald IL, Langrock R (2016) Hidden Markov models for time series: An introduction using R. 2nd edition. Chapman & Hall/CRC Press, Boca Raton

TABLES

Table 1. Transmitter numbers, sex, tag region, disc width (DW), number of detections (N detections), and tagging date for cownose rays *Rhinoptera bonasus* tagged with acoustic transmitters in the Chesapeake Bay and Georgia coastal waters. For two rays, DW was not recorded (NR) before release.

Transmitter	Sex	Tag region	DW (mm)	N detections	Tagging date
A69-1601-12703	Female	VA Chesapeake	940	77	5/29/14
A69-1601-12705	Male	VA Chesapeake	910	102	6/18/14
A69-1601-12706	Female	VA Chesapeake	935	173	5/28/14
A69-1601-12707	Female	VA Chesapeake	935	48	5/29/14
A69-1601-12708	Female	VA Chesapeake	968	35	5/29/14
A69-1601-17557	Female	VA Chesapeake	1012	107	7/23/14
A69-1601-17559	Male	VA Chesapeake	873	166	7/24/14
A69-1601-17560	Female	VA Chesapeake	905	35	8/20/14
A69-1601-17561	Female	VA Chesapeake	955	391	7/23/14
A69-1601-17562	Female	VA Chesapeake	955	664	8/20/14
A69-1601-17563	Female	VA Chesapeake	920	238	8/20/14
A69-1601-17564	Female	VA Chesapeake	975	109	7/24/14
A69-1601-17565	Female	VA Chesapeake	865	60	7/24/14
A69-1601-17567	Female	VA Chesapeake	950	187	8/20/14
A69-1601-17568	Female	VA Chesapeake	925	286	8/20/14
A69-1601-17605	Female	VA Chesapeake	990	563	10/13/14
A69-1601-17606	Female	VA Chesapeake	995	2000	10/13/14
A69-1601-17607	Female	VA Chesapeake	965	302	10/13/14
A69-1601-17608	Female	VA Chesapeake	960	20	10/13/14

A69-1601-17610	Female	VA Chesapeake	910	1349	8/20/14
A69-1601-17611	Male	MD Chesapeake	882	72	8/7/14
A69-1601-17612	Male	MD Chesapeake	811	77	8/7/14
A69-1601-17620	Female	VA Chesapeake	983	49	10/13/15
A69-1601-17621	Female	VA Chesapeake	965	210	10/13/15
A69-1601-27591	Male	Savannah	NR	367	8/4/14
A69-1601-28356	Male	Savannah	945	73	8/5/14
A69-9001-21836	Female	VA Chesapeake	945	390	10/13/15
A69-9001-21837	Male	MD Chesapeake	1005	132	6/1/16
A69-9001-21838	Female	VA Chesapeake	962	921	10/13/15
A69-9001-21839	Female	VA Chesapeake	880	512	10/13/15
A69-9001-21840	Male	VA Chesapeake	845	1602	10/13/15
A69-9001-21841	Female	VA Chesapeake	952	231	10/13/15
A69-9001-21842	Female	VA Chesapeake	805	66	10/13/15
A69-9001-21843	Female	VA Chesapeake	1018	287	10/13/15
A69-9001-21844	Male	MD Chesapeake	NR	108	6/21/16
A69-9001-21846	Female	MD Chesapeake	1035	3351	9/16/15

Table 2. Selection criteria (log-likelihood) for hidden Markov model (HMM) variations used to classify movement behaviors of cownose rays *Rhinoptera bonasus* based on acoustic tag detections.

Model	Log-likelihood
HMM	-5877.7
HMM + Velocity	-5668.24
HMM + Velocity + Elapsed Days	-5568.61
HMM + Velocity - Angle	-3806.63
HMM + Velocity + Elapsed Days - Angle	-3702.48
3-state HMM	-5337.39
3-state HMM + Velocity	-5233.31
3-state HMM + Velocity + Elapsed Days	-5180.26
3-state HMM + Velocity - Angle	-3477.98
3-state HMM + Velocity + Elapsed Days - Angle	-3443.59

Table 3. Mean ± standard deviation (SD) variables in each state classified by 3-state hidden Markov model of cownose ray *Rhinoptera bonasus* movement behavior with one-way ANOVA results. Letters in parentheses indicate significantly different groupings from Tukey's HSD analysis comparing means between states.

	State Mean ± SD			ANOVA		
Variable	State 1	State 2	State 3	F	df	p
Distance (km)	0.06 ± 0.42 (A)	4.27 ± 5.54 (A)	303.07 ± 336.17 (B)	318.70	2, 1094	<0.0001
Velocity (km/d)	0.01 ± 0.06 (A)	2.22 ± 2.65 (B)	13.10 ± 12.05 (C)	359.90	2, 1094	<0.0001
Elapsed Days	2.17 ± 3.04 (A)	3.04 ± 468 (A)	36.66 ± 38.68 (B)	298.60	2, 1094	<0.0001

Table 4. Mean ± standard deviation (SD) latitude and longitude (decimal degrees) of cownose rays *Rhinoptera bonasus* in each tagging region by time period. Periods were delineated based on movement behavior state using results of ANOVA. Letters in parentheses indicate significantly different groupings from Tukey's HSD analysis comparing means between states.

	MD Chesapeake	VA Chesapeake	Savannah	ANOVA	
Period	Mean ± SD Latitude (°N)			F_{df}	p
Winter	28.53 ± 0.03 (A)	28.42 ± 0.23 (A)	28.51 ± 0.03 (A)	$0.95_{2,68}$	0.392
Migratory	34.04 ± 3.64 (A)	32.91 ± 3.63 (A)	29.82 ± 1.58 (B)	$12.35_{2,272}$	<0.0001
Summer	38.66 ± 0.94 (A)	37.49 ± 0.62 (B)	32.00 ± 0.01 (C)	$8532_{2,794}$	<0.0001
	Mean ± SD Longitude (°W)				
Winter	80.45 ± 0.02 (A)	80.50 ± 0.09 (A)	80.43 ± 0.01 (A)	$1.84_{2,68}$	0.166
Migratory	78.20 ± 2.28 (A)	78.63 ± 2.08 (A)	80.73 ± 0.38 (B)	$14.83_{2,272}$	<0.0001
Summer	76.41 ± 0.63 (A)	76.39 ± 0.37 (A)	81.05 ± 0.01 (B)	$1579_{92,794}$	<0.0001

Table 5. Original assigned tagging region, total number of daily positions, and percentage of daily positions classified to each region based on mean latitude and longitude using linear discriminant analysis for each tagged cownose rays *Rhinoptera bonasus* detected during May-June in the Chesapeake Bay. Rays identified using transmitter numbers (Ray ID). Rays classified to a region other than their original tagging region indicated by bold type.

				Predicted Region (%)		
Ray ID	Date tagged	Assigned region	Total days detected	MD Chesapeake	VA Chesapeake	Assigned region
12706	05/28/14	VA Ches	6	0.00	100.00	100.00
17557	07/23/14	VA Ches	5	20.00	80.00	80.00
17559	07/24/14	VA Ches	22	0.00	100.00	100.00
17561	07/23/14	VA Ches	2	0.00	100.00	100.00
17562	08/20/14	VA Ches	20	0.00	100.00	100.00
17563	08/20/14	VA Ches	3	0.00	100.00	100.00
17567	08/20/14	VA Ches	5	0.00	100.00	100.00
17568	08/20/14	VA Ches	7	14.29	85.71	85.71
17605	10/13/14	VA Ches	73	0.00	100.00	100.00
17606	10/13/14	VA Ches	59	0.00	100.00	100.00
17607	10/13/14	VA Ches	32	0.00	100.00	100.00
17610	08/20/14	VA Ches	32	0.00	100.00	100.00
17611	**08/07/14**	**MD Ches**	**4**	**25.00**	**75.00**	**25.00**
17612	08/07/14	MD Ches	2	50.00	50.00	50.00
21836	**08/05/14**	**VA Ches**	**8**	**75.00**	**25.00**	**25.00**

21837	06/01/16	MD Ches	12	75.00	25.00	75.00
21838	10/13/15	VA Ches	18	5.56	94.44	94.44
21839	**10/13/15**	**VA Ches**	**5**	**80.00**	**20.00**	**20.00**
21840	**10/13/15**	**VA Ches**	**18**	**88.89**	**11.11**	**11.11**
21843	10/13/15	VA Ches	4	25.00	75.00	75.00
21844	**06/21/16**	**MD Ches**	**6**	**33.33**	**66.67**	**33.33**
21846	09/16/15	MD Ches	22	90.91	9.09	90.91

Table 6. Mean ± standard deviation (SD) latitude and longitude among tagged cownose rays *Rhinoptera bonasus* detected in May-June during the years of 2015 and 2016, with one-way ANOVA results comparting between years. Rays identified using transmitter numbers (Ray ID). Degrees of freedom (df) for latitude and longitude =1, df on table represents degrees of freedom for daily positions.

Ray ID	2015 mean ± SD	2016 mean ± SD	F_{df}	p
17559	37.24685 ± 0.00138	38.37305 ± 0.07207	$4622.8_{1,18.12}$	<0.0001
17605	37.26816 ± 0.02271	37.26364 ± 0.00690	$1.53_{1,54.26}$	0.221
17606	37.30283 ± 0.02687	37.26260 ± 0.22508	$0.22_{1,6.02}$	0.653
17607	37.28066 ± 0.06149	37.22354 ± 0.11772	$2.43_{1,14.67}$	0.141
27591	32.00768 ± 0.00698	32.00203 ± 0.00427	$23.44_{1,89.19}$	<0.0001
17559	76.50646 ± 0.00116	76.54368 ± 0.05374	$9.07_{1,18.15}$	0.007
17605	76.52787 ± 0.02710	76.52251 ± 0.00924	$1.46_{1,56.80}$	0.231
17606	76.57374 ± 0.03805	76.44031 ± 0.2231	$2.47_{1,6.05}$	0.166
17607	76.5377 ± 0.12128	76.48918 ± 0.17345	$0.72_{1,17.53}$	0.406
27591	81.04513 ± 0.00836	81.05199 ± 0.00496	$24.68_{1,88.25}$	<0.0001

FIGURE CAPTIONS

Figure 1. Mean daily positions of tagged cownose rays *Rhinoptera bonasus* based on 2014-2016 acoustic tag detections. Original tagging regions in MD Chesapeake, VA Chesapeake, and Savannah indicated by color. The farthest north and south detections are near Long Island, NY and St. Lucie Inlet, FL, respectively. No detections indicates the approximate locations of receiver arrays for which we confirmed that our rays were not detected.

Figure 2. Dates of mean daily positions for each of 28 tagged cownose rays *Rhinoptara bonasus* detected over periods greater than 90 days. Detections classified based on tagging region and identified by color.

Figure 3. Mean daily latitude (decimal degrees) of cownose ray *Rhinoptera bonasus* acoustic tag detections by date (May 2014-December 2016). Detections classified based on tagging region and identified by color.

Figure 4. A) Mean daily positions and modeled behavioral states from 3-state Hidden Markov modeling results of a single individual cownose ray *Rhinoptera bonasus* representative of each tagging region. Ray A69-9001-21840 was originally tagged in the VA Chesapeake region but showed a migration extent more representative of a MD Chesapeake ray. Behavioral states identified by color. B) Latitude and longitude (decimal degrees) by day of year for tagged cownose rays *Rhinoptera bonasus* classified by movement behavioral state as determined using 3-state Hidden Markov modeling. Behavioral states identified by color.

Figure 5. Mean probability of cownose rays *Rhinoptera bonasus* showing a Migratory behavioral state by day of year for each tagging region. Lines represent transitions between greater than or

less than 50% of locations classified as Migratory behavior. Red represents transitions during summer, blue represents transition periods during winter.

Figure 1.

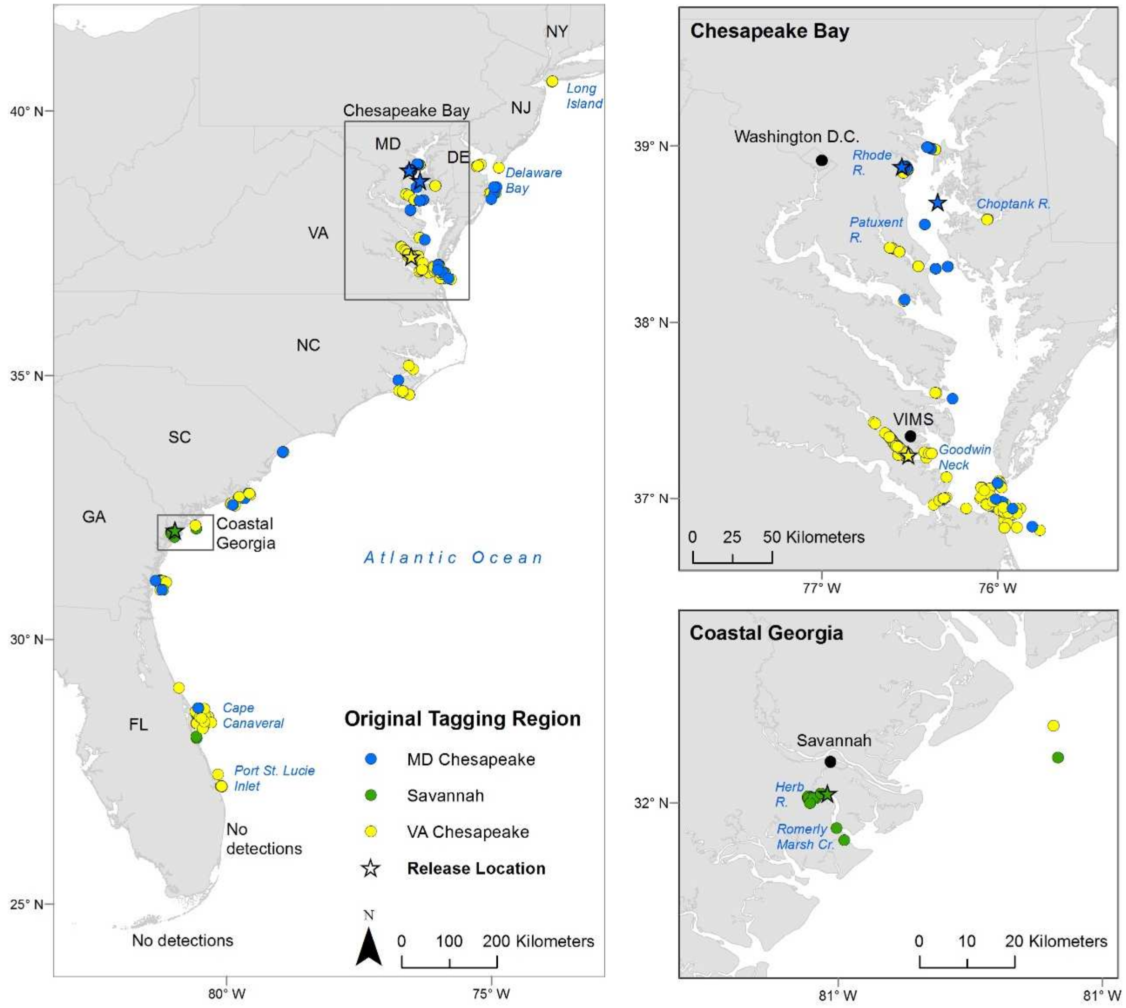
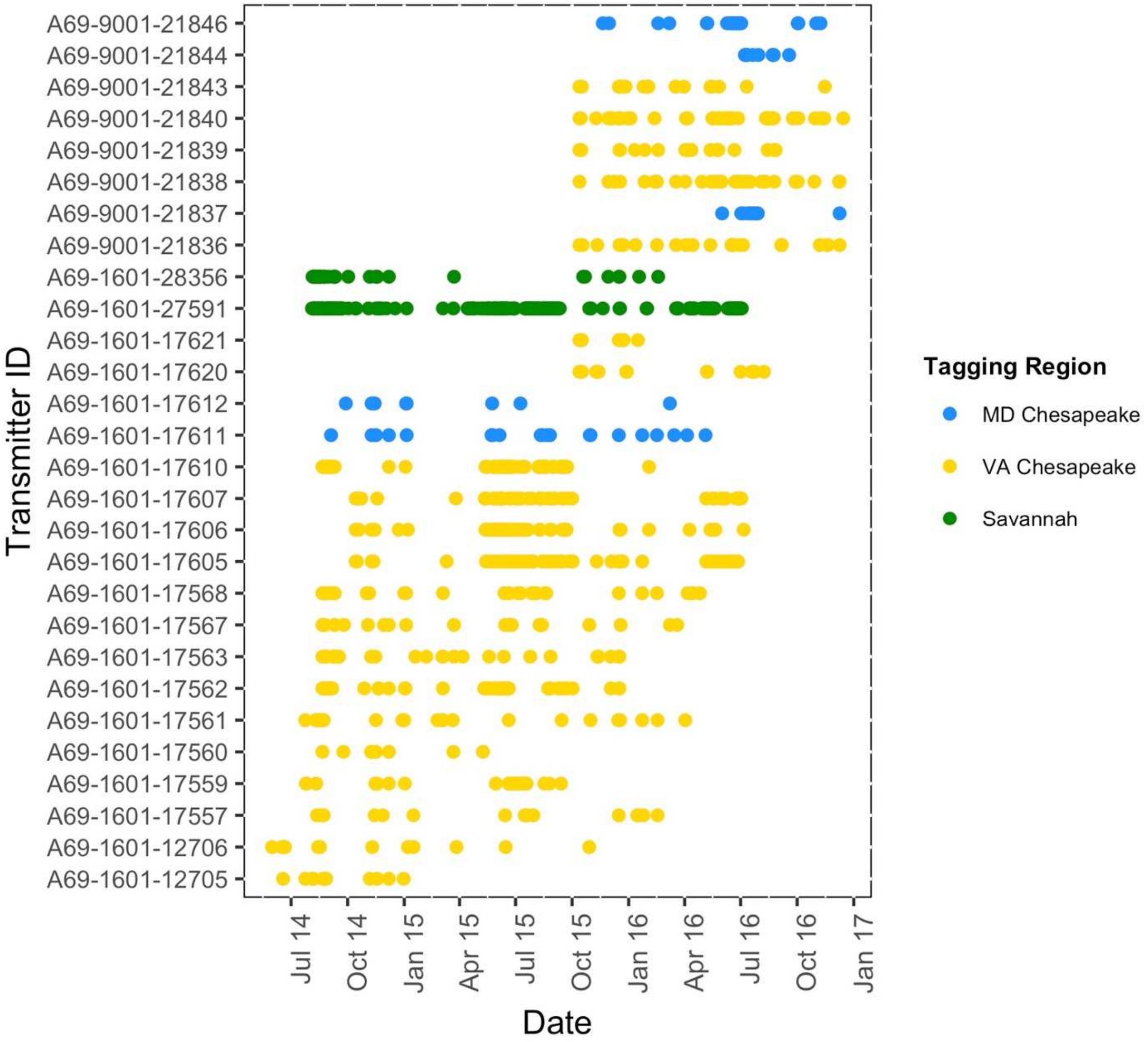
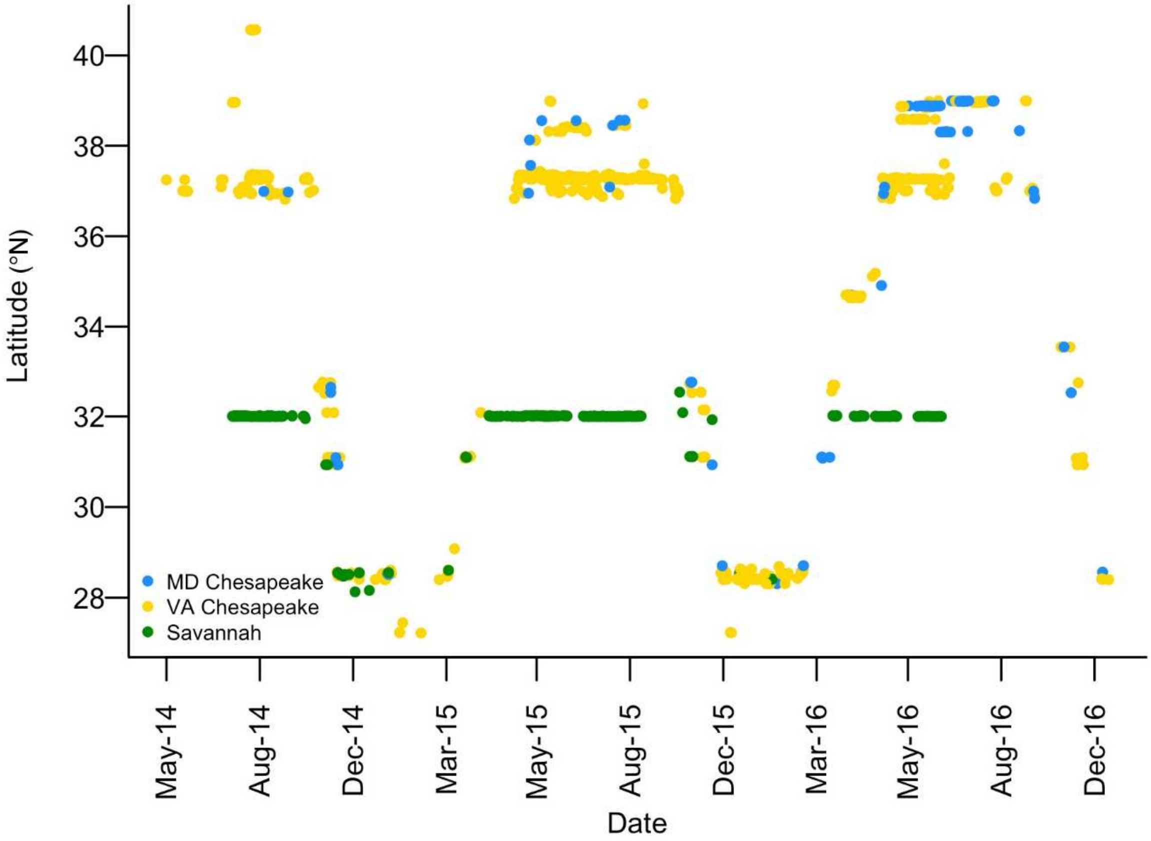

NY
Long Island
40° N
Chesapeake Bay
NJ
MD
DE
Delaware Bay
VA
NC
35° N
SC
GA
Coastal Georgia
Atlantic Ocean
30° N
Cape Canaveral
FL
Port St. Lucie Inlet
No detections
25° N
No detections
Original Tagging Region
● MD Chesapeake
● Savannah
● VA Chesapeake
☆ Release Location
N
0 100 200 Kilometers
80° W
75° W
Chesapeake Bay
39° N
Washington D.C.
Rhode R.
Choptank R.
Patuxent R.
38° N
VIMS
Goodwin Neck
37° N
0 25 50 Kilometers
77° W
76° W
Coastal Georgia
Savannah
32° N
Herb R.
Romerly Marsh Cr.
0 10 20 Kilometers
81° W
81° W

Figure 2.


Transmitter ID
A69-9001-21846
A69-9001-21844
A69-9001-21843
A69-9001-21840
A69-9001-21839
A69-9001-21838
A69-9001-21837
A69-9001-21836
A69-1601-28356
A69-1601-27591
A69-1601-17621
A69-1601-17620
A69-1601-17612
A69-1601-17611
A69-1601-17610
A69-1601-17607
A69-1601-17606
A69-1601-17605
A69-1601-17568
A69-1601-17567
A69-1601-17563
A69-1601-17562
A69-1601-17561
A69-1601-17560
A69-1601-17559
A69-1601-17557
A69-1601-12706
A69-1601-12705
Jul 14
Oct 14
Jan 15
Apr 15
Jul 15
Oct 15
Jan 16
Apr 16
Jul 16
Oct 16
Jan 17
Date
Tagging Region
MD Chesapeake
VA Chesapeake
Savannah

687 Figure 3.



688

689

Figure 4.

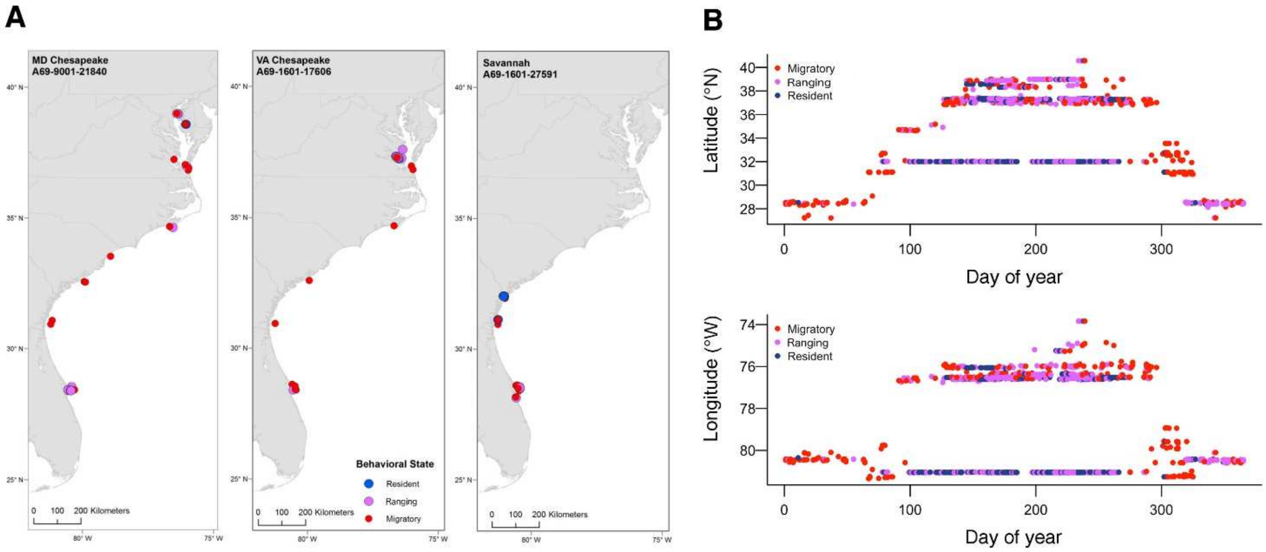
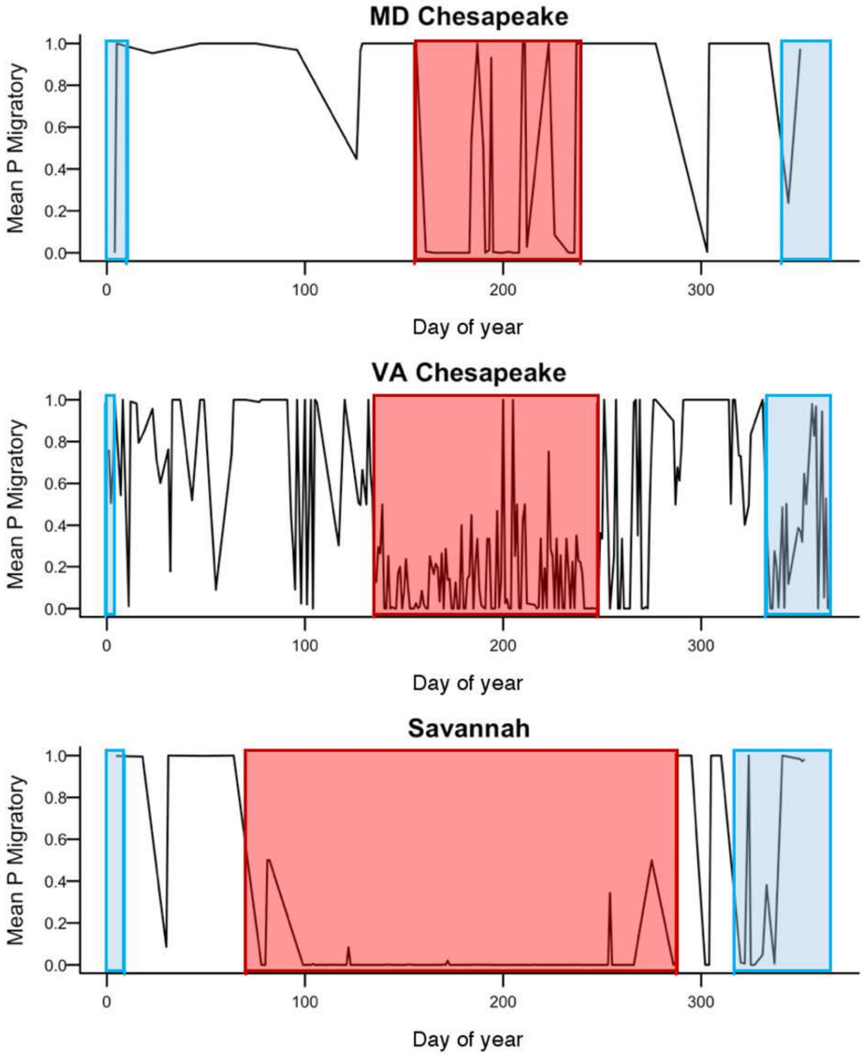
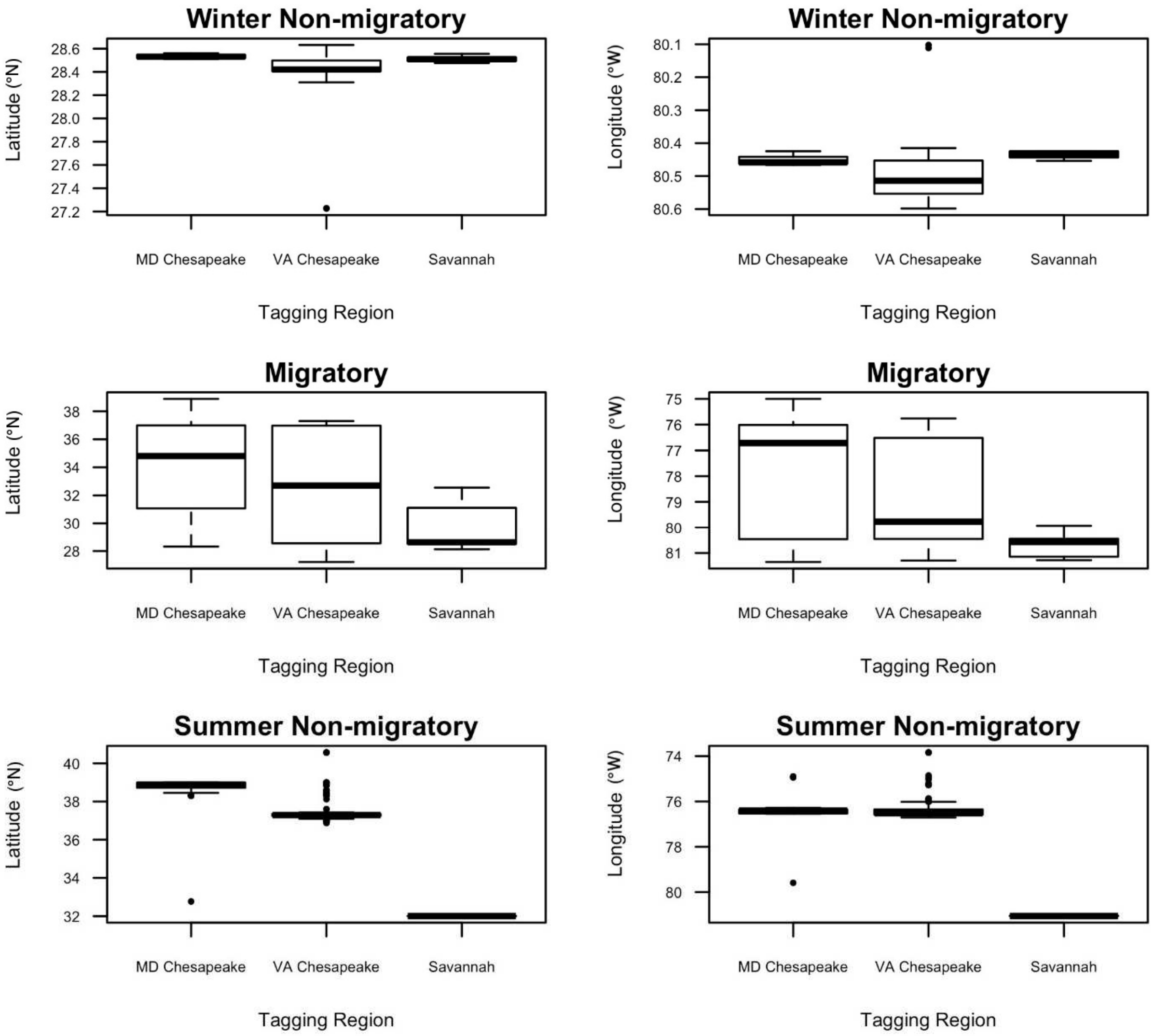

A
MD Chesapeake
A69-9001-21840
VA Chesapeake
A69-1601-17606
Savannah
A69-1601-27591
40° N
35° N
30° N
25° N
80° W
75° W
0 100 200 Kilometers
Behavioral State
Resident
Ranging
Migratory
B
Latitude (°N)
40
38
36
34
32
30
28
Day of year
0
100
200
300
Longitude (°W)
74
76
78
80
Migratory
Ranging
Resident

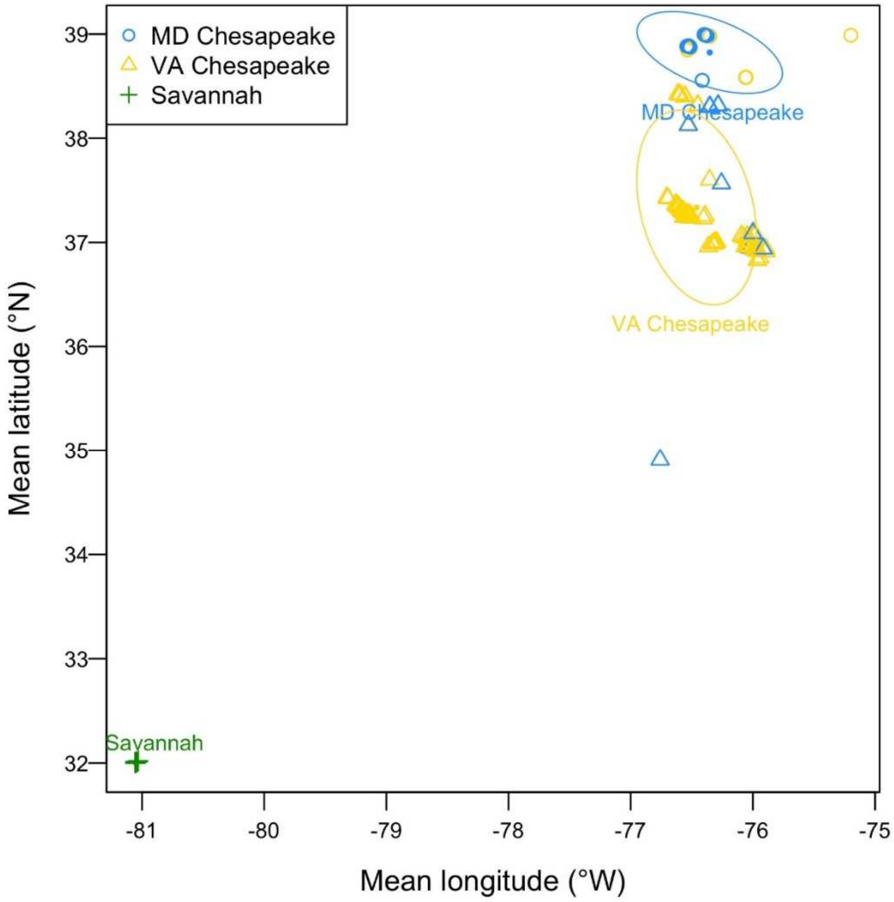
Figure 5.


MD Chesapeake
Mean P Migratory
1.0
0.8
0.6
0.4
0.2
0.0
0
100
200
300
Day of year
VA Chesapeake
Mean P Migratory
1.0
0.8
0.6
0.4
0.2
0.0
0
100
200
300
Day of year
Savannah
Mean P Migratory
1.0
0.8
0.6
0.4
0.2
0.0
0
100
200
300
Day of year

Supplemental figure 1. Boxplots of latitude and longitude (decimal degrees) of tagged cownose rays *Rhinoptera bonasus*. Data grouped by tagging region and behavioral period including winter non-migratory (Resident and Ranging behavioral states combined), migratory (spring and fall), and summer non-migratory periods.



Supplemental figure 2. Mean latitude and longitude of tagged cownose ray *Rhinoptera bonasus* daily positions during May-July. Symbol colors correspond to original assigned tagging region and symbol shapes correspond to predicted summer region based on linear discriminant analysis (LDA) classifications. Ellipse (95% confidence interval) and center point (mean) colors correspond to LDA classifications of predicted summer region. For example, yellow circles represent rays originally tagged in Virginia (indicated by yellow symbol) that were assigned by LDA to Maryland (symbol is a circle), and which were grouped within the Maryland 95% confidence ellipse (blue ellipse). Note that the Savannah ellipse is tiny and obscured by the symbols for the two Savannah rays.



Supplemental figure 3. Number (N) of individual tagged cownose rays *Rhinoptera bonasus* detected on each acoustic telemetry receiver with at least one tag detection. Note that the locations of acoustic receivers with zero ray detections are not shown because there is no comprehensive list of receiver locations for this region.